

Bryozoan-Mollusk Relationships

BY

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(Plate 40)

THE NATURE OF BRYOZOAN-MOLLUSK relationships has received considerable attention within the past four decades (BALSS, 1924; LECOINTRE, 1929, 1933; DOUVILLE, 1931; ROGER & BUGE, 1948; OSBURN, 1957; DUNCAN, 1957). The results of most of these earlier investigations were, however, contradictory. In general, two opposing schools of thought have developed. The first regards bryozoan-mollusk associations as primarily fortuitous, while the other maintains that bryozoan species are very specific in their choice of a substrate. Proponents of this latter view (DUNCAN, 1957; MOORE, 1963) have generally advocated that each particular bryozoan species is capable of successfully encrusting one species of mollusk only and that most bryozoan-mollusk associations are either symbiotic (BUGE, 1952), commensal or amensal (DUNCAN, 1957).

OSBURN (1950, 1957) was perhaps the most vociferous proponent of the first view. He stated (1957, p. 1109), that bryozoans ordinarily show little "choice" of a substratum, and that, in general, any firm and clean object will serve. He observed (*op. cit.*, p. 1110) over 30 species of bryozoans attached to a single large *Pinna* shell, and also pointed out that CANU & BASSLER determined more than 90 species from a single bryozoan haul.

DEICHMANN (1954) after studying the bryozoans encrusting the "Texas longhorn shells" from the Florida waters similarly concluded (DEICHMANN, *op. cit.*, p. 77) that the bryozoans were independent of mollusk shells as substrates. These records are, however, not compatible with views expressed by a larger number of other authors who have generally argued in favor of the host-specificity of most bryozoan species.

DUNCAN (1957) recently published an excellent summary of our knowledge of fossil bryozoans and devoted considerable attention to a discussion of the nature of their biotic associations. She concluded (*op. cit.*, p. 789)

that certain bryozoan species "almost invariably incrust only one kind of shell", and that the ability of a bryozoan species to completely enclose the encrusted substrate was indicative of the fact that the substrate was animate and mobile. A similar view was expressed by MOORE (1963, p. 88; pl. 32, fig. 1), who reported a "*Membranipora* sp." that forms a coating as much as nine millimeters in thickness on the gastropod *Searlesia? carlsoni* (ANDERSON & MARTIN, 1914) in the Astoria Formation of Oregon. She observed that the bryozoan was not found encrusting any other gastropod, although *Priscofusus medialis* (CONRAD, 1865) occurred in close association, in a similar environment and seemed to offer the same relative shape.

The problem of host specificity was carried a step farther by KIRKPATRICK & METZELAAR (1922) who described a *definite*, beneficial association between the multilamellar bryozoan species, *Conopeum commensale* KIRKPATRICK & METZELAAR, 1922, and the hermit crab *Petrochirus granulimanus* MIERS (= *Pagurus granulimanus* (MIERS)). They affirmed that the bryozoan-hermit crab association "appears to be a *definite* and not an accidental one, the crustacean and Polyzoan being more to each other than casual messmates; for it is certain they derive special advantages from each other's presence . . . the Polyzoan obviously benefits; for it is in alliance with a vigorous and successful marauder, and although sedentary by nature, is continually being carried to new and rich pastures." Because these authors failed to observe the bryozoan species on living mollusks from the same locality, they tentatively concluded (*op. cit.*, p. 988) that the bryozoan can possibly survive only for a short time and with much diminished vitality on an untenanted gastropod shell.

Data currently being assembled by the writer (though presently incomplete) are yielding very interesting results that tend to show that cheilostomatous bryozoans, at least, are not host specific. The author has confined his attention to a study of multilamellar cheilostomes only

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(see Plate 40). The advantage of this approach is that it is possible to observe not only the diversity of hosts encrusted by any single species but also the nature of the relationship of the many-layered colony of zoecia to the encrusted host. The latter can be more accurately inferred only by studying the large overgrown forms.

The materials in the collections of the Museum of Paleontology, University of California, Berkeley, currently being studied by the writer, include several large, ball-like, multilamellar colonies ranging in age from the Late Miocene (Santa Margarita Formation) to the Recent. The largest of these are over 2 inches in diameter (see Plate 40, Figures 3 and 5). By studying the gross morphology and thin sections of a few of these it is possible to make a few valid inferences. These preliminary results and their relationship to previously published views (discussed earlier) are discussed briefly below.

- 1) It was observed that at any single locality, members of a single bryozoan species encrust a diverse array of substrates. Such diverse substrates encrusted include different genera and species of gastropods (Figures 4 and 5), pelecypod shell fragments (Figures 1 and 2), and coarse-grained, arkosic sandstone fragments (Figure 3). This observation is, thus, in support of views earlier expressed by OSBURN (1957, p. 1109), but contradicts DUNCAN's (1957) and MOORE's (1963) idea that most bryozoan species encrust one kind of shell only.
- 2) In species that encrust gastropod shells, various stages representing gradual but continuous closure of the aperture is demonstrable (see Figures 4 and 5). Though the earliest formed zoecial layers follow the irregular contour of the encrusted substrate faithfully (see Figures 1 and 3), the tendency is for the bryozoan mass to finally assume a spherical shape (Figures 3 and 5). This observation indicates that while it is possible for a bryozoan to encrust an initially living shell, continued existence of the living mollusk is not required for continued thriving of the bryozoan. The implications of this observation are further discussed below. The tendency for the bryozoan to smother the host, overgrow its aperture and assume a spherical shape indicates that the relationship between them is certainly not advantageous to both.
- 3) The bryozoans tend to cover the encrusted substrate completely (Figures 1 to 5) irrespective of the fact that such substrate was initially animate (pelecypod and gastropod), or inanimate (shell fragment and sandstone fragment). This is, by far, the most important observation. DUNCAN (1957, p. 789) contended that the fact that bryozoans could completely cover an encrusted shell was good evidence that the former encrusted only

the shells of living mollusks. Her conclusion is, however, negated by the fact that these bryozoans encrust not only whole (Figure 2), but fragmentary shells (Figure 1) which could not have been part of a living mollusk when it was initially encrusted. The same bryozoan species also encrusts and completely encloses inanimate sandstone fragments (Figure 3). Additionally, these colonies appear to thrive equally well on molluscan as well as on sandy substrates (Figures 3 and 5). From this, it is possible to infer that not only have the bryozoans no need for an animate substrate at the start but also that any animate object that is initially encrusted or that secondarily inhabits such encrusted substrate (such as hermit crabs in gastropod shells) will eventually be smothered. Thus, the hermit crab inhabiting an encrusted gastropod shell will either get sealed within the shell by the rapidly expanding bryozoan or will escape before being sealed in, to find another shell. Even if we assume that the hermit crab is capable of keeping the molluscan aperture free by actively removing new zoecia deposited across it, its association with the bryozoan appears to be far from advantageous.

Thus, the author's present study tends to indicate that cheilostomatous bryozoans are not substrate-specific. The same species indiscriminately encrusts a diverse array of animate and inanimate objects. Bryozoan species can completely enclose a substrate even if the latter is non-animate. Finally, it is very likely that bryozoan-mollusk relationships are, at best, only fortuitous. Their reported restriction to one particular type of host or substrate is probably an oversight caused by inadequate sampling.

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Explanation of Plate 40

Membraniporid Bryozoans (? *Conopeum* spp.) Encrusting Diverse Substrates.

Figure 1: Hypotype, Univ. Calif. Mus. Paleo. no. 12160, x 2. Locality A-742. Late Miocene, Santa Margarita Formation, La Panza Quadrangle, San Luis Obispo County, California. "From south $\frac{1}{4}$ corner of Sec. 9, T. 29S., R. 17E." Thin section of a bryozoan colony encrusting a fragment of a pectinid shell. Note disc-like shape of colony and the undulations coinciding with the position of ribs. Parts of the outer edge of the specimen were lost during preparation. - Figure 2: Hypotype, UCMP no. 32886, x $\frac{3}{8}$. Locality B-6411. Pleistocene, San Pedro Formation, San Pedro Quadrangle, Los Angeles County, California. Collected from sandstones halfway between Harbor Freeway and Gaffey Street, about 100 to 300 feet south of Union Oil Refinery, San Pedro, California. Massive colony completely encrusting a valve of the pelecypod *Pseudochama exogyra* (CONRAD, 1837). Other colonies of the same species encrusting different gastropod shells were collected from the same locality. - Figure 3: Hypotype, UCMP no. 12159, x 2. Locality A-741. Late Miocene, Santa Margarita Formation, La

Panza Quadrangle, San Luis Obispo County, California. From Waterfalls, near the county road in the S. W. $\frac{1}{4}$ of Sec. 22, T. 29S. R. 17E. Thick succession of zooecial layers encrusting an irregular arkosic sandstone fragment. Note that, as in Figure 1, earliest formed layers follow the irregular topography of the encrusted surface. - Figure 4: Hypotype, UCMP no. 32883, x 0.9. Locality A-4454. Recent, Tumaco, Colombia, South America. Collected between Tumaco and the mouth of Rio Rosario. Massive colony encrusting an *Epitonium*-like gastropod. Note that aperture is still open but shows evidence of continued closure by zooecia. - Figure 5: Hypotype, UCMP no. 12158, x 1 $\frac{1}{2}$. Locality A-9731. Late Miocene, Santa Margarita Formation, Joaquin Rocks Quadrangle, Fresno County, California. From an orange to buff, sand and clay bed with abundant sand-filled borings on the bank of Domingine Creek in the N. W. $\frac{1}{4}$ of the S. W. $\frac{1}{4}$ of Sec. 33, T. 18 S., R. 15E. Massive colony completely enclosing a gastropod shell over whose aperture a zooecial layer over one inch thick was formed.

